



NEUROPTERIS OBTUSA, A RARE BUT WIDESPREAD LATE CARBONIFEROUS PTERIDOSPERM

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ABSTRACT. A rare but widespread neuropterid of Westphalian D and Stephanian age, *Neuropteris obtusa* (Brongniart) comb. nov., is redescribed from specimens from north-west Spain and Saarland, Germany. Its synonymy includes *Neuropteris raymondii* Zeiller, '*Mixoneura*' *subraymondii* Wagner, '*Callipteris*' *discreta* Weiss, and *Neuropteris thompsoniana* Darrah. Pustules in the interveinal areas of the pinnules in some specimens are interpreted as the probable result of fungal attack by rusts, although that they are glands cannot be excluded.

COMPRESSION/impresion remains of neuropterid foliage from the Carboniferous (and early Permian?) have recently received detailed attention with reference to the type species of *Neuropteris* Brongniart (Laveine and Blanc 1996) and the general classification of the group (Cleal and Shute 1995). The genus *Neuropteris* has been restricted and several new genera distinguished on the basis of frond architecture and (where known) cuticle characters. Where such characters are absent, species can only be assigned to these genera by comparing their morphology with that of better known species.

It is important to solve problems of synonymy in such pteridosperms if their stratigraphical and phytopalaeogeographical usefulness is to be maximized. In the present paper, a rare but apparently widespread species, *Neuropteris obtusa* (Brongniart) comb. nov., known under various different generic and specific names from the Westphalian D and Stephanian, is analysed on the basis of remains from north-west Spain and Saarland. Understanding this species is also important because its basionym (*Odontopteris obtusa* Brongniart, 1831) has played a role in the definition of the genus *Mixoneura* Weiss. Some of the Spanish specimens have pinnules with 'pustules' in the interveinal areas, which we believe are probably evidence for fungal attack by rusts.

MATERIALS AND METHODS

The specimens described here from the Stephanian of north-west Spain, are penultimate and last order pinna fragments belonging to a single species of probable pteridosperm. All are preserved on silty and slightly silty mudrock. On weathered surfaces (localities 1176, 1181, 1184, 1301, 1821, 2706, 9584) they are impressions with little or no organic matter left. Specimens from a coal tip (loc. 931) and from boreholes (3689, 4563, 5366) are compressions preserving black organic material, but which is too highly carbonized to yield cuticles. All the figured specimens have been photographed with oblique lighting, partly with a Pentax SFX autofocus reflex camera equipped with a 100 mm macrolens in daylight, and partly (at higher magnifications) under a Zeiss preparation microscope with camera attachment with artificial lighting.

Two specimens from Saarland, representing part and counterpart of the type of '*Callipteris*' *discreta* Weiss, 1870, are an imprint on shale. These were photographed by Prof. M. Barthel with artificial lighting.

LOCALITIES AND REPOSITORIES

The Spanish localities are all on the southern flank of the Cantabrian Mountains, north-west Spain, where an almost complete succession of Stephanian strata is developed. These localities are identified by numbers. Where not stated otherwise, the repository is the Palaeobotanical Collections at Jardín Botánico de Córdoba (Spain). Catalogue numbers prefixed GT for Guardo-Tejerina and CM for Ciñera-Matallana.

Tejerina Syncline

About 1000 m thickness of early Cantabrian strata is exposed in the valley and gorge north of the village of Tejerina, north of Prioro (León province, north-west Spain). A description of this section was originally published by Wagner *et al.* (1969); the environment of deposition has been discussed by Iwaniw (1985a). Of the more than 60 plant localities sampled from this section by Wagner (see Wagner and Winkler Prins 1985, p. 391), only three have yielded remains of *Neuropteris obtusa*.

1181 – Oejo Formation, Cerroso Member. North-eastern part of the Tejerina Syncline, in the quartzite conglomerate interval cropping out north of the main road to Prioro (León). Age: early Cantabrian. Catalogue numbers GT 00056–00067.

1184 – Oejo Formation, Cerroso Member. Intercalated shales in the top part of the conglomerate formation north of Tejerina, about 600 m north of the village. Age: early Cantabrian. Catalogue number GT 00046.

1821 – Prado Formation, 110 m above the base of the formation, north of Tejerina village (compare Wagner and Winkler Prins, 1985, p. 378, fig. 11). Age: early Cantabrian. Forty-two specimens: catalogue numbers GT 00001–00042 (including Pls 2–4). Specimens recorded as *Mixoneura raymondii* by Wagner in Wagner *et al.* (1969).

Guardo Coalfield

The extensively sampled Guardo Coalfield (Palencia and León provinces, north-west Spain), representing the same basin as Tejerina, has provided four additional localities.

2706 – Tarilonte Formation, Villaverde de la Peña (Palencia). Age: late Westphalian D. Catalogue numbers GT 00043–00044.

9584 – Tarilonte Formation, middle part of Las Heras section (Palencia). Age: late Westphalian D. Catalogue number GT 00068.

1176 – Prado Formation, road-wall locality about 500 m west-north-west of Valderrueda (León). Age: early Cantabrian. Catalogue numbers GT 00047–00055 (GT 00047 recorded as *Odontopteris* cf. *robusta* by Wagner 1964a, pl. 1, figs 2, 2a).

5366 – Antracitas de Besande, Grupo Minero La Espina (León), borehole 18 *bis*. Age: early Cantabrian. Catalogue number GT 00045.

Ciñera-Matallana Coalfield

The Stephanian B strata of the Ciñera-Matallana Coalfield (León province, north-west Spain) have been described by Wagner (1971), who defined the various formations recognized within a total succession thickness of about 1500 m. The Stephanian B in the sense of the Carmaux succession of the Massif Central (France) is not the same as the Stephanian B *sensu* St Etienne, which is later in age.

931 – San Francisco Formation, tip of the San Francisco coal mine near the village of Correcillas. Age: Stephanian B. Three specimens (figured as *Mixoneura subraymondii* Wagner, 1964b, pl. 10, figs

21–23) are in the Museo Nacional de Ciencias Naturales, Madrid, catalogue numbers V-2576 and V-2821–V-2822. One specimen lodged in Madrid (Wagner, 1964*b*, pl. 11, figs 24, 24a) has apparently been lost. Seven specimens (including counterparts of Pl. 5, figs 4–6, and Pl. 6, figs 1–5) are in the Jardín Botánico de Córdoba, catalogue numbers CM 00001–00007.

1301 – Cascajo Formation, *c.* 3 m above the *Leaia* band at the base of the formation; roadside locality between Villalfeide and Correcillas. Age: Stephanian B. Specimen mentioned as *Mixoneura subraymondii* in Wagner (1964*b*, p. 15). Catalogue number CM 00008.

3689 – Cascajo Formation, 18 m above the base of the formation, borehole S 26 (Sociedad Hullera Vasco-Leonesa) in the Vegacervera Syncline, near the synclinal core. Age: Stephanian B. One specimen (part and counterpart). Catalogue numbers CM 00009–00010 (Pl. 5, fig. 3; Pl. 6, fig. 6). 4563 – Pastora Formation, 60 m below the base of the Cascajo Formation, borehole S 41 (S. H. V. L.), at 698 m depth. Borehole in the southern flank of Matallana Syncline. Age: Stephanian B. Catalogue number CM 00011 (Pl. 5, figs 1–2).

Saarland (Germany)

Amelung coal seam (Westphalian D), Von der Heydt colliery, near Saarbrücken. An imprint in shale recorded originally by Weiss (1870). Collection of the Museum für Naturkunde, Paläontologisches Institut, Berlin, catalogue number 1212.

SYSTEMATIC PALAEOLOGY

Order TRIGONOCARPALES Seward, 1917 or MEDULLOSALES Němejc, 1950

Form-genus NEUROPTERIS Brongniart, 1822

Remarks. This genus, introduced by Brongniart (1822, p. 233) as the section *Neuropteris* of the general form-genus *Filicites*, has been restricted by Cleal *et al.* (1990) to only part of the wider grouping which is traditionally recorded under the name *Neuropteris* (cf. Cleal and Shute 1995). *Neuropteris sensu stricto* comprises dichotomous fronds with monopinnate pinnae of several orders with intercalated pinnae being present on the main rachis above the dichotomy; lateral pinnules are attached by a single point or by part of the basal width; generally anomocytic stomata, prominent intercellular flanges and trichomes on the abaxial pinnule surface, and a clear differentiation between costal and intercostal cells on the adaxial surface (Cleal *et al.* 1990).

Brongniart (1828, 1831, p. 250) introduced the form-genus *Odontopteris* for bipinnate fronds with the pinnules adhering to the rachis by their entire basal width, and the veins ascending directly from the rachis without or almost without the intervention of a midrib. The type species is the well-known Stephanian element *Odontopteris brardii* Brongniart. Cleal *et al.* (1990) observed that the frond architecture as based on *Odontopteris minor-zeilleri* Potonié (a synonym of *O. brardii*, according to Wagner 1964*b*) is similar to that of *Neuropteris sensu stricto*, and that the epidermal structure is also the same, with the exception of a more random orientation of the stomata in *Odontopteris*.

Weiss (1869) distinguished *Mixoneura* as a subgenus of *Odontopteris*, with *Odontopteris obtusa* Brongniart as the type species. However, he interpreted this species in the sense of Brongniart's (1831) plate 78, figure 3 which does not belong to the same taxon as Brongniart's (1831) plate 78, figure 4, the holotype of *Odontopteris obtusa*. Brongniart's plate 78, figure 3 and Weiss's (1869) specimens are generally assigned to *Odontopteris lingulata* (Göppert) Schimper, which is a possible synonym of *Odontopteris subcrenulata* (Rost) Zeiller. It is noted that the species grouped around *Mixoneura lingulata* form a sufficiently characteristic complex to justify *Mixoneura* as a form-genus in its own right. However, Zeiller (1906) and, above all, Bertrand (1930) used *Mixoneura* for neuropterid species with partly odontopteroid pinnules, i.e. pinnules which are broadly attached to the rachis, in the upper parts of pinnae. This modification of Weiss's (sub)genus has created a

certain amount of confusion, and this has caused most authors to abandon the term *Mixoneura*. *Mixoneura*, in Bertrand's usage, refers to the group of *Neuropteris ovata* Hoffmann, which forms part of *Neuropteris* as restricted by Cleal *et al.* (1990). Bertrand's different usage is to be regretted because *Mixoneura* Weiss, as originally described, refers to *Mixoneura lingulata* and similar species, which is a fairly closely circumscribed group that may well be retained as a separate genus. The members of this genus constitute a morphologically cohesive group of species, which correspond palaeoecologically to plants that seem to have lived in the better drained habitats, i.e. mesophile plants.

Potonié (1893, p. 133) later introduced *Neurodopteris* as a form-genus transitional between *Neuropteris* and *Odopteris*. He compared it with *Mixoneura* Weiss, a genus which he rejected since he regarded it as being part of *Odopteris*. Potonié (1893) based *Neurodopteris* on the species *Neuropteris auriculata* Brongniart, a form which is quite different from the species grouped around *Mixoneura lingulata*. Zeiller (1906) considered *Neurodopteris* to be synonymous with *Mixoneura*, which he interpreted as a morphogenus showing characters intermediate between *Neuropteris* and *Odopteris*. He referred *Neurocallipteris neuropteroides* (Göppert) Sterzel to *Mixoneura*. Potonié (1907) assigned '*Mixoneura*' *neuropteroides* to *Neurodopteris*, and regarded *Neurocallipteris* Sterzel (1895) as a synonym. Nowadays, on considering the various type species of the genera *Mixoneura*, *Neurodopteris*, and *Neurocallipteris*, it is apparent that these three form-genera may well be distinguished as separate entities. Cleal and Shute (1995), when discussing the various neuropterid genera, considered *Neurodopteris* and *Neurocallipteris*, but did not comment on *Mixoneura*.

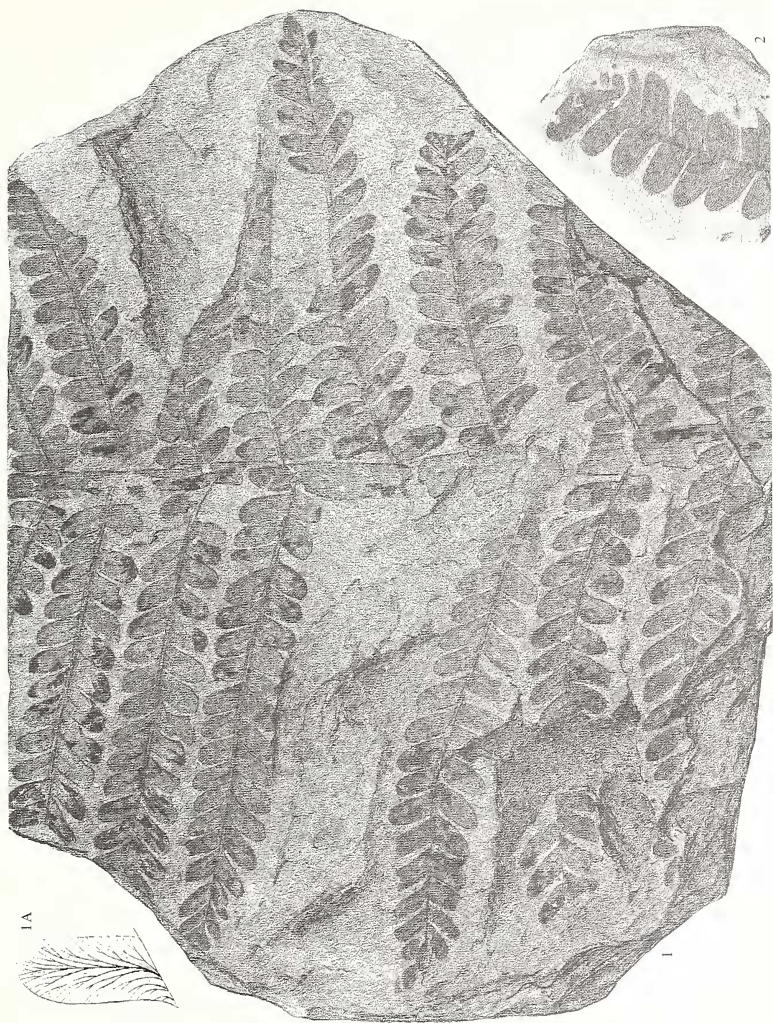
Neuropteris obtusa (Brongniart) comb. nov.

Plates 2–6

- * 1831 *Odopteris obtusa* Brongniart *pars*, p. 255, pl. 78, fig. 4 (*non* fig. 3 [= *Odopteris suberenulata* (Rost) Zeiller or *Odopteris lingulata* (Göppert) Schimper]. [Basionym].
non 1869–72 *Odopteris obtusa* Brongniart; Weiss, p. 36, pl. 3, figs 1–5 [= *Mixoneura lingulata* (Göppert) comb. nov.]; pl. 6, fig. 12 [= *Neurocallipteris neuropteroides* (Göppert) Cleal, Shute and Zdzrow?].
- * 1870 *Callipteris discreta* Weiss, p. 872, pl. 20, figs 1–2.
* 1888 *Odopteris obtusa* Brongniart; Zeiller, in Renault and Zeiller, p. 224, pl. 23, figs 1, 1A, 2, 2A–B [fig. 2 = reillustration of holotype].
* 1890 *Neuropteris raymondi* Zeiller, p. 147, pl. 9A, fig. 4.
* 1904 *Odopteris obtusa* Brongniart; Potonié, II-23, 1 fig.
* 1913 *Alethopteris discreta* (Weiss) Franke (*pars*), 173, figs 1–2 (*non* figs 3–4 [= *Gondomaria grandeuryi* (Zeiller) comb. nov.]).
* 1956 *Neuropteris raymondi* Zeiller; Doubinger, p. 114, pl. 12, fig. 3; pl. 13, fig. 1 [both photographic reproductions of the holotype].
?* 1961 *Odopteris glandulosa* Remy and Remy, p. 1, pl. 1, figs 1–11.
1964a *Odopteris cf. robusta* Zalesky; Wagner, pl. 1, figs 2, 2a.
* 1964b *Mixoneura subraymondi* Wagner, p. 10, pl. 10, figs 21–22; pl. 11, figs 23–24.
1969 *Mixoneura raymondi* (Zeiller) Wagner, in Wagner *et al.*, p. 124, pl. 1, figs 1–2a.
* 1969 *Neuropteris thompsoniana* Darrah, p. 99, pl. 54, fig. 2.
* 1970 *Neuropteris raymondi* Zeiller; Doubinger, p. 279, pl. 15, fig. 4 [holotype].
?* 1971 *Odopteris glandulosa* Remy and Remy; Doubinger and Germer, p. 135, pl. 7, fig. 6 [reillustration of Remy and Remy 1961, pl. 1, figs 1–2, 5–6].

EXPLANATION OF PLATE I

Figs 1–2. *Neuropteris obtusa* (Brongniart) comb. nov.; copy of *Odopteris obtusa* as figured by Zeiller (1888, pl. 23); × 1 (except 1A, × 3). 1, 1A, Commeny (France). 2, Brongniart's holotype; Terrasson near Brive (France).



WAGNER and CASTRO, *Neuropteris*

- 1981 *Odontopterus alpina* (Sternberg) Geinitz; Fritz and Boersma, p. 394, figs 7–8.
 ?1985 *Odontopterus obtusa* Brongniart; Iwaniw, pl. 4, fig. 5.
 1986 *Odontopterus alpina* (Sternberg) Geinitz; Fritz and Boersma, p. 255, fig. 20.

Description. Pinnae of the penultimate order showing a flat rachis, up to 8 mm wide (Pl. 1, fig. 1), and closely spaced pinnae of the last order (Pl. 2, fig. 3). Thin rachis of the last order (0.3–0.5 mm wide), apparently rounded in cross section. Pinna terminals gradually tapering, with progressively more broadly adherent pinnule bases, and possessing a relatively small but well individualized apical pinnule, which tends to become rhombic (Pl. 2, figs 3, 5).

Pinnules variable in length/breadth ratio and also in the insertion, which ranges from adherence at a single point to, more commonly, a partial or even full adherence of the pinnule base to the rachis. Pinnule length 7–20 mm, at 3–7 mm width, with a length/breadth ratio of *c.* 2.2–2.5. Pinnules in the basal part of pinnae are attached by a strongly decurrent stalk, which is almost reclined on to the rachis, and thus simulates a partial adherence to the rachis; these pinnules are ovoid, with rounded (cordate) bases. However, higher up in the pinnae, the pinnule bases fuse with the rachis, with the decurrent midrib lying subparallel to the rachis, and the lateral veins arising from the partially and sometimes wholly fused decurrent midrib; this creates the impression of the lateral veins being derived from the rachis on the basicopic side of pinnules that are rather asymmetrical. The pinnules in the higher parts of pinnae show a decurrent base on the basicopic side, whilst the acroposcopic side is still contracted to some extent. In the uppermost parts of pinnae, the pinnule bases slope downwards to such an extent as to form a narrow band of limb along the rachis.

Veining pattern is characterized by a thin, decurrent midrib which dissolves into even thinner, although well-marked, lateral veins at about half-way to one-third up the pinnule length. Lateral veins arise from the midrib at a very narrow angle; they are broadly arching and dichotomize at least twice, often even three times, before reaching the pinnule margin at angles of generally *c.* 60° (varying between 50° and 80°). Widely spaced lateral veins (16–37 veins/10 mm) reach the pinnule margin at fairly regular intervals (which become more irregular where vein splits occur near the pinnule margin).

A rounded, rather large *Cyclopterus* pinnule (Pl. 4, fig. 3), has been found in association.

Comparisons. *Neuropteris subauriculata* Sterzel is another species with pinnules showing a decurrent midrib and, in the upper parts of pinnae, a tendency towards partial fusion of the pinnule bases with the rachis. The illustrations by Remy and Remy (1959) show a higher nervation density, and *Neuropteris subauriculata*, as figured by Daber (1955), shows rather massive terminals. The presence of large triangular pinnules and of pinnae with *Cyclopterus* pinnules suggests a comparison with *Neuropteris ovata* Hoffmann and similar species. However, epidermal characters support the attribution to *Macroneuropteris*, as proposed by Cleal *et al.* (1990) (see also Cleal and Shute, 1995, p. 23). The difference between this species and *Neuropteris britannica* Gutbier is not very clear. The latter species has also been referred to *Macroneuropteris* by Cleal *et al.* (1990).

Odontopterus jeanpaulii Bertrand (= *O. alpina sensu* Geinitz, *non* Sternberg) (see Daber 1955, pl. 24, figs 1, 1a) is also quite similar, although this species possesses very large pinnules. Remy and Remy (1977, p. 294, fig. 167) apparently rejected Bertrand's species, and referred its type specimen back to *Odontopterus alpina* (Sternberg) Geinitz. Doubinger and Grauvogel-Stamm (1980) also rejected the introduction of *Odontopterus jeanpaulii*, and admitted the correctness of Geinitz's (1855) identification of his specimens with '*Neuropteris*' *alpina* Sternberg. The illustrations provided by Daber (1955), Remy and Remy (1959, 1977) and Doubinger and Grauvogel-Stamm (1980) show pinnules which are broadly attached to the rachis. The veins are markedly bundled, showing up to

EXPLANATION OF PLATE 2

Figs 1–6. *Neuropteris obtusa* (Brongniart) comb. nov; loc. 1821, near Tejerina (León, north-west Spain); Prado Formation (lower Cantabrian). 1–3, 5–6, GT 00001; two last order pinnae belonging to the pinna of the penultimate order (previously figured in Wagner *et al.* 1969, pl. 1, fig. 1, 1a) showing pinnules with decurrent basicopic and constricted acroposcopic sides; pinna terminal and lateral pinnules enlarged to show details of venation; carbonized dots between veins interpreted as masses of resting spores of rusts. 4, GT 00003; pinna fragment. 1–2, 5–6, ×6; 3–4, ×3.



WAGNER and CASTRO, *Neuropteris*

four successive dichotomies. They are very widely spaced, *c.* 14–15 veins/10 mm. The pinnule apices are less rounded than those of *Neuropteris obtusa*, and the veins are less arched, more repeatedly forked, and more widely spaced than in *N. obtusa*. Doubinger and Grauvogel-Stamm (1980, pl. 4) illustrated a dense array of spots in between veins, which they interpreted as hairs or glands. They did not consider the possibility of fungal attack (rusts). The specimens figured as *Odontopteris alpina* by Fritz and Boersma (1981, 1986) are here attributed to *Neuropteris obtusa*.

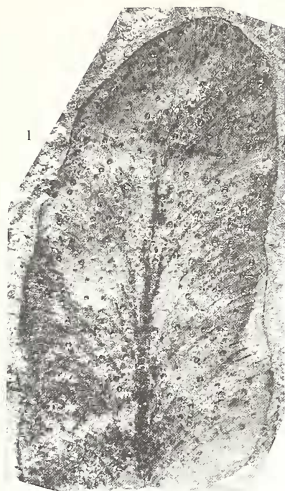
Odontopteris robusta Zalesky, a similar species, was figured originally only with a diagrammatic drawing (Zalesky, 1934, p. 1113). A natural size photograph of a different specimen was added subsequently by Novik (1952, pl. 59, fig. 1). Both illustrations refer to material from the type area (Donbass in southern Russia and Ukraine). Although these illustrations are too poor to be judged adequately, the accompanying description by Zalesky (1934, p. 1112), mentions broadly attached pinnules with a decurrent basicopic side and a slightly contracted acroscopic side, as well as a venation which is characterized by a well-defined midrib reaching two-thirds up the pinnule length, and repeatedly forked, arching lateral veins. Terminals to the pinnae of the last order are shown as rather massive, with a large, well-developed apical pinnule. A rather similar specimen from the Guardo Coalfield of north-west Spain has been figured photographically by Wagner (1983, pl. 7, fig. 2; pl. 8, fig. 1). It has only been identified tentatively in view of the poor illustration of the holotype, which is consequently difficult to use. Another specimen (Wagner 1964a, pl. 1, figs 2, 2a), from the same coalfield, is here included in the synonymy of *Neuropteris obtusa*. The possibility exists that '*Odontopteris obtusa*' and '*Odontopteris robusta*' are the same species. Not only are the pinnule shape and insertion fairly comparable, but the nervation is quite similar. Insofar as a vein count is feasible, Zalesky's drawing shows *c.* 18 veins/10 mm, which is within the range recorded for *Neuropteris obtusa*. A similar vein density is recorded for the specimens figured by Wagner (1983) as *Odontopteris cf. robusta*. Zalesky (1934) provided only a description, not making any comparisons. Novik (1952) made comparison with *Odontopteris kryshstofovichii* Novik, but the latter seems to be a mariopterid; thus making the comparison irrelevant.

The rounded apices and the tendency to show a contraction at the acroscopic side, make the pinnules of *Neuropteris obtusa* and *Odontopteris robusta* different from those of *Odontopteris brardii* Brongniart, which are characterized by a rather marked asymmetrical shape, and generally more acute apices.

Remarks on synonymy. *Odontopteris obtusa* Brongniart was based on two specimens, which the author of the species already perceived as belonging to two different entities. Brongniart (1831, p. 255) designated his plate 78, figure 4 as the type. The other specimen (Brongniart, 1831, pl. 78, fig. 3) was attributed by Zeiller (*in* Renault and Zeiller 1888, p. 227) to *Odontopteris lingulata* (Göppert) Schimper, a species that had been illustrated by Weiss (1872, pls 2–3) as *Odontopteris obtusa* (note that the specimen figured on Weiss's pl. 6, fig. 12 is different, *i.e.* possibly belonging to *Neuocallipteris neuropteroides* (Göppert) Cleal, Shute and Zdzrow). Weiss (1869, p. 36) placed *Neuropteris subcrenulata* Rost, 1839 in synonymy, and the same suggestion was made by Zeiller (1888, p. 227). Weiss (1869, p. 36; 1870, p. 864) used his (incorrect) interpretation of *Odontopteris*

EXPLANATION OF PLATE 3

Figs 1–3. *Neuropteris obtusa* (Brongniart) comb. nov.; small carbonized dots irregularly distributed on the pinnule; loc. 1821 near Tejerina (León, north-west Spain); Prado Formation (lower Cantabrian). 1, GT 00009; single pinnule showing venation. 2, GT 00020; pinnules with a decurrent base on the basicopic side, and a constriction on the acroscopic side, a midrib up to about half-way along the pinnule length, and broadly arching lateral veins; note the apparent irregularity in scatter of small dots of carbonized organic material between veins. 3, GT 00004; fragment of penultimate pinna with relatively small, more-or-less ovoid pinnules with constricted bases, particularly in lower part of pinnae; pinnules higher up pinnae show progressive fusion of the basicopic sides with the rachis, thus tending to become asymmetrical and decurrent; midrib thin; broadly arching, repeatedly forked lateral veins. All $\times 6$.



obtusa Brongniart as the type of the form-genus *Mixoneura* Weiss, which he introduced as a subgenus of *Odontopteris*. Since he based his concept on *Odontopteris lingulata* and not on the real *Odontopteris obtusa*, as represented by the holotype (as designated by Brongniart, 1831, p. 255, as 'le véritable type'), the mention by Andrews (1970, p. 133) of *Odontopteris obtusa* as the type species of *Mixoneura* is formally correct but misleading in the absence of a reference to the misidentification involved. The synonymy of '*Odontopteris lingulata*' and '*Odontopteris subcrenulata*' used to be regarded as well-established, and this is why *Mixoneura subcrenulata* (Rost) is generally mentioned as the type of the form-genus *Mixoneura* (compare Wagner 1964b, p. 8). However, Doubinger and Remy (1958) distinguished between '*Odontopteris lingulata*' and '*Odontopteris*' (alias: *Neuropteris*, *Mixoneura*) *subcrenulata*, and regarded these species as different taxa. They further distinguished between three varieties of *O. subcrenulata*, viz. var. *subcrenulata*, var. *gallica* Doubinger and Remy, and var. *elongata* Doubinger and Vetter. The subtle differences between the three varieties of *Mixoneura subcrenulata* on the one hand and *Mixoneura lingulata* on the other require well-pressed material for a proper differentiation. If one accepts the criteria described by Doubinger and Remy (1958) as valid, the type species of *Mixoneura* Weiss is *Mixoneura lingulata* (Göppert) comb. nov. (basonym: *Neuropteris lingulata* Göppert, 1846, p. 104, pl. 8, figs 12–13). Since Doubinger and Remy (1958) reported *Odontopteris lingulata* as being restricted to the lower Rotliegendes of the Saar-Nahe Basin and of Thuringia, this would apparently exclude Brongniart's plate 78, figure 3, which was from Terrasson in the Brive region, south-central France. However, they may have simply overlooked Brongniart's specimen, which is not discussed in their paper. Whatever the problems with the recognition of the different taxa in the *Mixoneura subcrenulata-lingulata* complex, it is clear that the specimen on Brongniart's plate 78, figure 3 (originally attributed to *Odontopteris obtusa* Brongniart) belongs to the *Mixoneura* complex and must be excluded from *Neuropteris obtusa* (Brongniart) comb. nov. All authors are agreed on this point.

Zeiller's (1888) more accurate rendering of the true holotype of *O. obtusa* has allowed a proper assessment of the characters of the lateral pinnules of this species. Along with the holotype, Zeiller (1888) also figured a more substantial specimen of '*Odontopteris obtusa*' from the upper Stephanian of the Commentry Coalfield in the Massif Central, France. Zeiller's illustrations are reproduced here as Plate 1. This larger specimen is a fragment of a pinna of the penultimate order with subopposite last order pinnae, which taper gradually and end in a small, rhombic, apical pinnule. The lateral pinnules are attached by the entire base, as is shown by the single pinnule figured at $\times 3$ enlargement (Zeiller 1888, pl. 23, fig. 1A), but there is a slight contraction on the acroscopic side. Zeiller's illustration (Pl. 1, fig. 1) also shows this. All pinnules are rather small (i.e. not longer than 10 mm, with a length/breadth ratio of about 2:1). The midrib is shown to be thin but well individualized to at least half-way up the pinnule, with arching lateral veins bundled into twice-forked units. The vein density is c. 24 veins/10 mm. Wagner (1964b, p. 14) mentioned that '*O. obtusa*' seemed to possess more broadly attached pinnules with a somewhat wider nervation than occurred in '*Mixoneura subraymondii*' (which was put at 29–37 veins/10 mm). However, the subsequent inclusion of '*Mixoneura raymondii*', with a lower vein density (16–25 veins/10 mm), and a more generous interpretation of the variation in pinnule morphology, apparently removes the objection to regarding all these remains as belonging to a single taxon.

The large specimen of '*O. obtusa*' figured by Zeiller (1888, pl. 23, fig. 1) with length/breadth pinnule ratios of about 2:1, may well represent the higher part of a pinna of the penultimate order, whereas the holotype of *Neuropteris raymondii* Zeiller, 1890 represents the lower part of a penultimate pinna. The latter shows more elongate pinnules (length/breadth ratio c. 3:1), with more constricted bases, but it displays a venation which is totally comparable to that of *Neuropteris obtusa*. The pinnules in the upper part of the pinnae of the last order of *N. raymondii* display the wide insertion that is characteristic of *N. obtusa*. It is very likely that *N. obtusa* and *N. raymondii* represent examples of the same species, and that the differences observed are due merely to different positions in the frond. Indeed, specimens of transitional characteristics, albeit closer to *N. raymondii*, occur in the Stephanian of north-west Spain (Wagner 1964b, under the name of *Mixoneura subraymondii* Wagner; Wagner, in Wagner et al. 1969, as *Mixoneura raymondii* (Zeiller)

Wagner; specimen reproduced here partially as Pl. 2, fig. 3). The thin midrib, the rather steep departure of the lateral veins from the midrib, their broadly arching course, and the repeated forking, are all characters shared between *N. obtusa* and *N. raymondii* (including *Mixoneura subraymondii*). The vein density of c. 25 veins/10 mm is also similar, as is the small rhombic terminal of the pinnæ of the last order. The only apparent difference is in the pinnule insertion, but this can be explained with reference to the position in the frond. If the synonymy between these three taxa is admitted, as the present writers do, *N. obtusa* has priority.

Another synonym is *Callipteris discreta* Weiss. This species was assigned to *Gondomaria* by Wagner and Lemos de Sousa (1982), but this is now perceived as having been in error. *Callipteris discreta* was introduced by Weiss (1870) on the basis of three specimens. The two figured specimens (compare the synonymy list), show a marked resemblance to *Neuropteris obtusa* in the shape and insertion of the pinnules as well as in the general pattern of the nervation (see Pl. 7, figs 1–3, which is the counterpart of Weiss, 1870, pl. 20, fig. 1). Since Weiss used the species name *obtusa* for the *Mixoneura lingulata* – *subcrenulata* complex, it probably did not occur to him to compare his material with '*Odontopteris obtusa* Brongniart *sensu stricto*'. *Callipteris discreta* Weiss was referred to *Alethopteris* by Franke (1913), who joined it with *Alethopteris grand'euryi* Zeiller. There is, indeed, a resemblance, particularly in the vein pattern, but the pinnules of Zeiller's species show more markedly decurrent bases and a length/breadth ratio of 3:5 to 4:1. Wagner and Lemos de Sousa (1982) accepted the wide sense in which '*Alethopteris discreta*' had been interpreted by Franke, and synonymized it with *Gondomaria alethifolia* Teixeira, 1964. However, the two species synonymized by Franke (1913) are probably two different taxa. Teixeira's *G. alethifolia*, from the upper Stephanian of Portugal, is apparently the same as *Alethopteris grand'euryi* as described by Zeiller (1888) from Commeny, and the correct combination should therefore be *Gondomaria grand'euryi* (Zeiller) comb. nov. (basonym: *Alethopteris grand'euryi* Zeiller, 1888). On the other hand, '*Alethopteris discreta*' Weiss is more properly assigned to *Neuropteris obtusa*. The specimens from the Westphalian of Portugal figured by Wagner and Lemos de Sousa (1982) as *Gondomaria discreta* (Weiss) are now believed to have been assigned incorrectly. Their proper identification is in abeyance, but it may be a fern and quite outside the group of fossils considered in the present paper, which are likely to be pteridosperms.

The holotype of *Neuropteris thompsoniana* Darrah, 1969 may be included in *Neuropteris obtusa*. Darrah suggested a comparison with *Neuropteris heterophylla*, but this species is obviously very different. The type is from the upper Westphalian D of Illinois, USA.

It is a matter of conjecture as to whether the small fragment figured and described by Remy and Remy (1961) as *Odontopteris glandulosa* may be assigned to *Neuropteris obtusa*. Not only is it a small fragment, but its venation is poorly preserved. However, it apparently shows the vein pattern known for *N. obtusa*. The justification for the recognition of this species as a special entity was the extensive covering by small dots, which Remy and Remy (1961) regarded as glands. They excluded the possibility that fungal attack was involved, but this is by no means clear to the present writers. Remy and Remy's interpretation was accepted by Doubinger and Germer (1971), who refigured the holotype of *O. glandulosa*. The same kind of dots appear in a number of specimens figured as *N. obtusa* in the present paper.

'*Odontopteris obtusa* Brongniart *sensu stricto*' has rarely been reported in the literature, and some of the records must be regarded as doubtful. The small fragment figured by Zeiller (1890) from the Autunian may have been identified correctly, but it seems too fragmentary for confident identification. The same problem attaches to the small fragment figured by Iwaniew (1985b). However, this fragment is from the same area in north-west Spain as most of the specimens figured herein. The specimen figured and described by Vetter (1968, p. 119, pl. 32, figs 1, 4) from the Stephanian of Decazeville, France, cannot be judged adequately from the illustrations, but does not conform to the species described here. The three fragments illustrated from Saarland as *Odontopteris obtusa* by Doubinger and Germer (1971, pl. 46, fig. 3a–c) are also excluded. Their vein density is too high. These specimens are also too small to be identified reliably. A North American (Dunkard) specimen figured by Darrah (1975, fig. 7) as *Odontopteris* cf. *obtusa* Naumann is

Odontopteris obtusiloba Naumann. Wagner and Lyons (1997) suggested that this specimen should be referred to *Odontopteris brardii* Brongniart. On the other hand, two specimens from the Stephanian of the Carnic Alps (Fritz and Boersma, 1981), recorded as *Odontopteris alpina*, clearly belong to *Neuropteris obtusa*. They show a marked resemblance to specimens recorded in the literature as *Neuropteris* (vel *Mixoneura*) *raymondii*.

Wagner (*in* Wagner *et al.* 1969, p. 125) compared '*Mixoneura*' *raymondii* (Zeiller) with a specimen figured as *Neuropteris* sp. by Germer *et al.* (1966, pl. 5), which was later described as *Neuropteris schaeferi* by Doubinger and Germer (1975). The more adequate illustration of this specimen by Doubinger and Germer (1975) shows a higher nervation density (*c.* 45 veins/10 mm), and allows a comparison with *Neuropteris ovata* Hoffmann, as is suggested also by the investigation of its cuticle by Saltzwedel (1968), as quoted by Cleal and Shute (1995, p. 28).

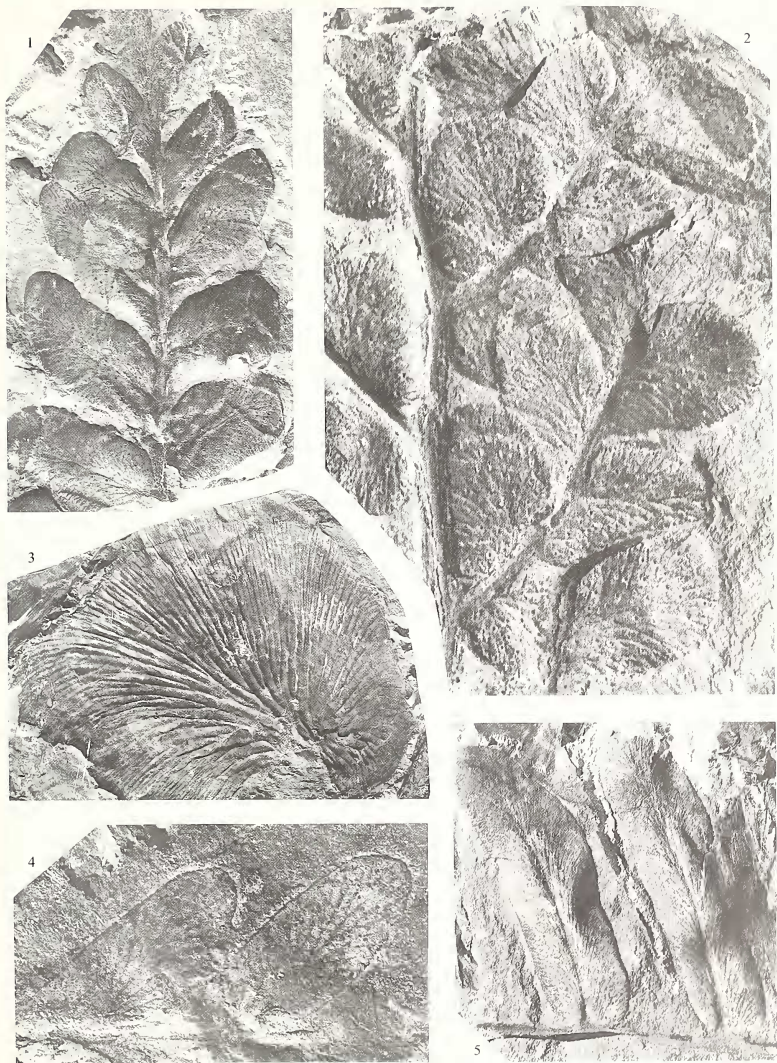
Remarks on generic assignment. The species dealt with in the present paper has been recorded variously as *Odontopteris*, *Neuropteris*, and *Mixoneura*, and it has been referred to various different species by the different authors. The distinctions apparently depended mainly on the position in the frond. The name *Mixoneura* is only applied properly to the species grouped around *Mixoneura lingulata* and *Mixoneura subcrenulata*, which are obviously quite different. The form-genera *Neuropteris* and *Odontopteris* were discussed most recently by Cleal *et al.* (1990), who pointed out the close similarities between these two genera, which are distinguished almost entirely on pinnule insertion and the virtual absence of a midrib in *Odontopteris*. Whereas this provides a reasonable distinction for the type species, *Odontopteris brardii* Brongniart, the presence of both neuropteroid and odontopteroid pinnules in the species dealt with in the present paper makes its attribution to either one or the other form-genus somewhat arbitrary. However, there may be merit in restricting *Odontopteris* to *O. brardii* and similar species (e.g. *Odontopteris minor* Brongniart and *Odontopteris reichiana* Gutbier), in which case the species described here is probably best regarded as *Neuropteris obtusa* (Brongniart) *comb. nov.* (basionym: *Odontopteris obtusa* Brongniart 1831 *pars*, as referenced in the synonymy list).

Remarks on figured specimens. Plate 2, figure 3 is a partial reproduction of the pinna of the penultimate order depicted in Wagner *et al.* (1969, pl. 1, fig. 1, 1a) as *Mixoneura raymondii* (Zeiller). This specimen is directly comparable to the larger fragment of a pinna of the penultimate order figured from Commentry in France by Zeiller (1888, pl. 23, fig. 1; Pl. 1), to which it could be attached to complete the upper part. This suggests a pinna up to *c.* 0.3 m long, with lateral pinnae (of the last order) 50–100 mm long. These two pinnae of the penultimate order show pinnules 6–10 mm long. The also very comparable remains figured by Weiss (1870) as *Callipteris discreta* (refigured as *Alethopteris discreta* by Franke 1913; Pl. 7, figs 1–3) are penultimate pinna fragments with slightly longer pinnules (up to 13 mm), whereas the holotype of *Neuropteris raymondii* Zeiller,

EXPLANATION OF PLATE 4

Figs 1–2, 4–5. *Neuropteris obtusa* (Brongniart) *comb. nov.*; interveinal dots interpreted as carbonized remains of resting spore masses of rusts. 1–2, 5, loc. 1821, near Tejerina (León, north-west Spain); Prado Formation (lower Cantabrian). 1, GT 00015; terminal part of pinna showing characteristically small apical pinnule and relatively broad lateral pinnules with partially fused, decurrent bases; $\times 3$. 2, GT 00016; presumably rather high part of a penultimate pinna with short, relatively broad pinnules showing partial fusion with the supporting rachis; $\times 6$. 5, GT 00019; exceptionally long pinnules, corresponding most probably to the lower part of a major pinna; pinnules constricted at both sides of the base; venation pattern and interveinal dots difficult to see at this enlargement; $\times 3$. 4, GT 00056; pinnules showing the venation and interveinal dots; loc. 1181, near Tejerina (León, north-west Spain); Oejo Formation (lower Cantabrian); $\times 6$.

Fig. 3. *Cyclopteris* assumed to belong to *Neuropteris obtusa* (Brongniart) *comb. nov.*, with which it was found in association. It shows an equally wide venation, but no interveinal dots; GT 00041; same locality as figs 1–2, 5; $\times 1$.



WAGNER and CASTRO, *Neuropteris*, *Cyclopteris*

1890 shows even longer pinnules (up to 16 mm). The shorter pinnules in the higher parts of pinnae are markedly odontopteroid, with a decurrent base on the basiscopic side, whereas the longer pinnules in the lower parts of pinnae show contracted bases on both the acroscopic and basiscopic sides, even though the basiscopic side is less heavily constricted. This type of pinnule is most obviously displayed by the holotype of *N. raymondii*, but it is also seen in the terminal part of a pinna of the last order figured by Wagner (*in Wagner et al.* 1969, pl. 1, fig. 2). These pinnule variations combined with the size variation of last order pinnae suggest that the frond was at least tripinnate, possibly about 0.7–0.8 m wide, with a total length in excess of 1 m.

The variation in pinnule size, length/breadth ratio, and insertion (more or less decurrent basiscopic side which is contracted in the pinnules lower down the pinnae) is shown by the specimens depicted from a single locality (Tejerina, loc. 1821) on Plates 2–4. These include both short, rounded, broadly inserted pinnules (Pl. 4, fig. 2) and rather elongate pinnules with constricted bases (Pl. 4, fig. 5).

Plate 7 of the present paper reproduces the counterpart of Weiss's (1870, pl. 20, fig. 1) specimen of '*Callipteris discreta* Weiss, from the Westphalian D of Saarland. This shows pinnules that are wholly comparable to the examples figured on Plate 5, figure 4, and Plate 6, figure 6, from the Stephanian B of north-west Spain.

Occurrence. Although *Neuropteris obtusa* is a rare species, the list of synonymy and the extensive illustration herein show it to have been widespread in Europe, with a stratigraphical range that embraces both Westphalian D (Saarland, Germany; Guardo Coalfield, north-west Spain) and the entire Stephanian (Massif Central, France; north-west Spain; Carnic Alps). The records by Brongniart (1831) and Zeiller (1888) are from the Stephanian C/lower Autunian in France, whilst Zeiller (1890) refers to the Stephanian B. The Spanish records are from lower down in the Stephanian, i.e. Cantabrian and Stephanian B (*sensu* Carmaux, which is lower than the type Stephanian B of St Etienne, both in the French Massif Central). The Stephanian C and lower Autunian in France probably represent the same time interval in different (independent) basins. The records from the Carnic Alps are from the (high) Stephanian of Schuler and Rattendorfer Alm in Kärnten, Austria (Fritz and Boersma 1981, 1986 – as *Odontopteris alpina*).

If *Neuropteris thompsoniana* Darrah is accepted as a synonym, *Neuropteris obtusa* occurs also in the upper Westphalian D of the Mazon Creek horizon (Francis Shale overlying Colchester No. 2 Seam, Desmoinesian), Illinois, in North America.

PROBABLE PARASITISM BY RUSTS

The lower Cantabrian locality 1821 at Tejerina (León province), north-west Spain, has yielded 22 remains of *Neuropteris obtusa* (originally called *Mixoneura raymondii* by Wagner, *in Wagner et al.* 1969), all with a fairly dense scattering of round elevations on the pinnule lamina (Pls 2–4). Specimens from locality 1181, also in the lower Cantabrian of Tejerina, show these 'pustules' too (Pl. 4, fig. 4). These rounded elevations occur invariably on the pinnule limb area in between veins and appear as carbonized dots even where the cuticle and other organic matter have disappeared as a result of oxidation by weathering. This suggests a dense array of organic matter in domed areas on the softer part of the pinnule lamina. There is no structure preserved and maceration (oxidation) would not have yielded any results in view of the fairly high rank of the coals in this area.

Three possibilities come to mind: (1) rusts, (2) possible glands, and (3) sporangia (sori). The last is ruled out in view of the positioning in between veins; sporangia would require a vascular

EXPLANATION OF PLATE 5

Figs 1–6. *Neuropteris obtusa* (Brongniart) comb. nov.; Ciñera-Matallana Coalfield (León, north-west Spain); Stephanian B. 1–2, CM 00011; loc. 4563; Pastora Formation. 3, 5–6, V-2821 (Museo Nacional de Ciencias Naturales, Madrid); pinnules previously figured as *Mixoneura subraymondii* Wagner (*in Wagner* 1964b, pl. 10, fig. 22, 22a), without 'pustules'; loc. 931; San Francisco Formation. 4, CM 00010; loc. 3689; Cascajo Formation. All $\times 6$.



connection. The second possibility is the one selected by Remy and Remy (1961) for their species *Odontopteris glandulosa*. This shows very similar structures to those found in the specimens figured in the present paper from locality 1821 (Pls 2–4). However, even though it cannot be rejected out of hand, this second possibility also seems unlikely to the present writers. The carbonized dots in between veins are irregularly distributed (see in particular Pl. 3, fig. 2), whereas glands would show a more regular pattern. It is also noteworthy that the remains described as *Mixoneura subraymondii* by Wagner (1964b), and assigned herein to *Neuropteris obtusa*, do not show rounded elevations in between veins. Assuming that the specimens from locality 931 in the Ciñera-Matallana Coalfield (i.e. '*Mixoneura*' *subraymondii*, as described by Wagner 1964b), are correctly assigned to the same species as occurs at locality 1821 at Tejerina (Wagner *et al.* 1969; Wagner and Winkler Prins 1985, p. 378), then it is apparent that the rounded elevations found on the pinnules of the specimens from Tejerina (loc. 1821) are not invariably present in this species. The preservation is equally good in both localities. Although it is possible to contend that the presence of glands is ecologically controlled, thus allowing for their presence or absence in the different localities, it is easier to assume that one is dealing with an element foreign to the plant. A comparison with rusts thus becomes the more reasonable assumption.

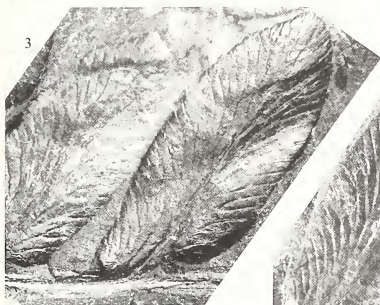
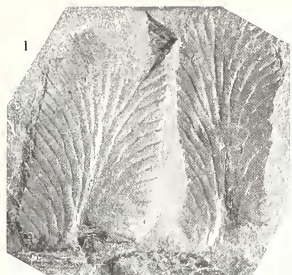
The same reasoning was applied by Göppert (1836, p. 262) when describing similar structures on *Hymenophyllites zobellii* Göppert (now *Palmatopteris zobellii* (Göppert) Potonié). He attributed these structures to 'Blattpilze' (rusts) and described these under the name of *Excipulites neesii* Göppert. The case was restated by Göppert (1841, pp. 55–56, pl. 5, figs 3–4), who refigured the same specimens. Göppert's explanation has been generally accepted. Carpentier (1937) figured and described similar dots on *Callipteris* (now *Autunia*) *conferta* (Sternberg) Brongniart. He referred these to *Excipulites* and admitted the likelihood of fungal attack, but left open the possibility of glands. Potonié (1893) pointed out that an anatomical investigation of these rounded elevations would be required so as to be absolutely certain. This is undoubtedly true, but requires a very low degree of maturity of the organic matter to make this a viable proposition. In the absence of absolute proof, one has to rely on analogy for the assumption that these are rusts.

Uredinales have a complicated life history, with five different stages, some of which are quite ephemeral. Some of these stages are characterized by fairly thick-walled spores occurring in sori which are apt to be preserved by carbonization, whereas others do not produce structures likely to be preserved in this manner. The resting stage, which is represented by teleutospores, is probably the one most likely to be preserved by carbonization. It lasts several months and the teleutospores possess relatively thick walls. Teleutospores are described as occurring either free or united laterally to form small groups, layers or columns (Alexopoulos *et al.* 1995). The teleutospore sori extend beyond the epidermis of the host (which they pierce), and are capable of forming small rounded elevations similar to the ones seen on the pinnules of *Neuropteris obtusa* from the lower Cambrian of Tejerina (locs 1181 and 1821). However, aecia (with aeciospores) and uredia (with uredospores) also form masses which pierce the epidermis of the host forming a kind of pustule. The drawing presented by Göppert (1836, pl. 36, fig. 4) is suggestive of an aecial cup with a peridium surrounding the spore chains. This kind of structure is not present in the material from Tejerina, which shows small rounded elevations, without any suggestion of a central depression. It thus seems most likely that these represent masses of teleutospores, if they are accepted as being rusts.

In the specimens from locality 1821 in the Tejerina section, these small elevations apparently

EXPLANATION OF PLATE 6

Figs 1–6. *Neuropteris obtusa* (Brongniart) comb. nov.; Ciñera-Matallana Coalfield (León, north-west Spain); Stephanian B. 1–5, V-2821, V-2576 and V-2822 (Museo Nacional de Ciencias Naturales, Madrid); pinnules previously figured as *Mixoneura subraymondii* Wagner (*in* Wagner 1964b, pl. 10, figs 22, 22b; 21, 21a; and pl. 11, figs 23, 23a, respectively), without 'pustules'; loc. 931; San Francisco Formation. 6, CM 00009; loc. 3689; Cascajo Formation. All $\times 6$.



cover the upper surface of the pinnules, where they occur in single rows of well-spaced dots in between the lateral veins. The spacing is irregular, even where the pinnule appears fully covered. Surface weathering has removed most of the organic matter, leaving the presumed resting spores of the rust as shiny dots of carbonized material on the convex surface of the pinnule. Where the carbonized elevations have been removed, a small rounded pit marks the position of each, thus showing that the probable spore mass partly protruded and partly occupied a position within the epidermis and the subepidermal area of the pinnules.

The possibility of fungal attack by rusts was first mentioned from the Carboniferous of Spain by Wagner (1964*b*) when describing material of *Mixoneura matallanae* Wagner. The presence of epiphytic fungi on *Sphenopteris biturica* Zeiller was mentioned by Doubinger and Alvarez-Ramis (1964), but the only specimen illustrated seems to show immature sporangia. Fernández-Marrón (1984) described fungal attack on certain plant fossils from the upper Westphalian of north-west Spain. She figured a specimen of *Linopteris obliqua* (Bunbury) Zeiller, which may indeed be assumed to have been infested by rusts. She also identified other cases of fungal attack, but these are rather less convincing. Fernández-Marrón (1984) suggested that certain specimens figured by Stockmans (1933), Laveine (1967) and Wagner (1965) would have suffered fungal attack, but this cannot be accepted since the specimens quoted show the adherence of *Spirorbis pusillus* Martin worm tubes. Iwaniew (1985*b*, pl. 1, fig. 3) figured probable rusts on a specimen of *Eusphenopteris neuropteroides* (Boulay) Novik from the lower Cantabrian of north-west Spain. Probable rusts on foliage remains of *Dicksonites* and '*Mixoneura*' *wagnerii* Lorenzo from the upper Stephanian of La Magdalena in north-west Spain were figured by Castro (1997), who discussed the phenomenon extensively. These examples are similar to the ones illustrated in the present paper.

Fungal hyphae were demonstrated in connection with Carboniferous pteridosperm leaf remains by Barthel (1961), who concluded on an ectoparasitic relationship. Although this proves that fungal activity on Carboniferous pteridosperm leaves did occur, the nature of Barthel's evidence is both different from and more convincing than ours.

CONCLUSIONS

The rare, but geographically widespread, Westphalian D and Stephanian species *Odontopteris obtusa* Brongniart is apparently the same as *Neuropteris raymondii* Zeiller, '*Mixoneura*' *subraymondii* Wagner, '*Callipteris*' *discreta* Weiss, and *Neuropteris thompsoniana* Darrah. This species is assigned to *Neuropteris* in the present paper.

It is assumed that this species was prone to fungal attack leading to the fossilized (carbonized) remains of masses of resting spores (teleutospores?) of rusts found as small rounded elevations in the interveinal areas of pinnules. Whether these elevations merit separate taxonomic treatment as *Excipulites* Göppert remains an open question. It is admitted that the structures interpreted as possible evidence of fungal attack by rusts, may also be interpreted as glands, a point difficult to resolve without microscopic preparations which are not feasible due to the relatively high degree of carbonization.

EXPLANATION OF PLATE 7

Figs 1–3. *Neuropteris obtusa* (Brongniart) comb. nov. MNIPB 1212; counterpart of type of '*Callipteris*' *discreta* Weiss, 1870; Saarland; Amelung coal seam (Westphalian D). 1, two last order pinnae showing pinnules with decurrent basispic and constricted acrosopic sides; $\times 2$. 2–3, lateral pinnules enlarged to show details of the venation, which are wholly comparable with pl. 5, fig. 4, and pl. 6, fig. 6, from the Stephanian B of Ciñera-Matallana; $\times 5$.



1



2



3

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